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Adult body size drives sexual selection mutually in the ladybird, *Menochilus sexmaculatus* (Coleoptera: Coccinellidae)

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Abstract:【Aim】Mate choice is a central process of sexual selection, and whenever fluctuations in the cost of reproduction and variance in mate quality occur, the traditional sex roles may also vary. In order to testify the thought that males can also be choosy like the females under certain circumstances, we studied male and female mating success in relation to adult body size as an indicator of fitness in *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae).【Methods】Small and large adults of both sexes were selected randomly from the stock culture and subjected to male and female mate choice trials. The offspring of successful pairs were also tested for their mating success by placing them in mate choice trials too.【Results】Mate choice experiments revealed the presence of size dependent mating success in both male and female mating trials. Males discriminated between the females on the basis of their quality, *i. e.*, body size which is an indicator of fecundity function. In female mating trials also large males achieved higher mating success than small males. Large females produced more eggs than did small females regardless of paternal size, and body size, however, did not influence egg viability. The offspring of large parents developed faster and lived longer than those of small parents, but did not display any advantage in terms of sexual desirability or competitiveness as mates when they were put in mate choice with the offspring from stock culture.【Conclusion】This study revealed the presence of mutual mate choice in this insect with size being the trait of interest.

Key words: *Menochilus sexmaculatus*; fitness; mate choice; mating success; reproductive output; sexual competitiveness

1 INTRODUCTION

The studies pertaining to sexual selection have mainly concentrated on the distinct reproductive roles of males and females characterised in terms of competitive males and choosy females. The evolutionary importance of sexual selection is well established as it manoeuvres fitness levels through preferential mating in favour of stronger and/or more attractive mates signalling better genes and higher fitness (Andersson, 1994).

In the past few years, a revival in the traditional theory of sex roles involving indiscriminate males seeking attention of choosy females has begun where even males tend to choose mates without offering any benefits to females or the offspring (Gwynne, 1991). Examples from past researches do confer the presence of male mate choice in species where they offer parental care (Gwynne, 1991). However, evidence for the presence of male mate choice in many species where male offer nothing significant to the offspring is also available (Bonduriansky, 2001).

The parental investment theory (Trivers, 1972) predicts that it is the level of investment made by the male or female that decides which sex will exhibit mate choice. However, in mating system where both the sexes do not contribute anything to parental care apart from the acquisition of good genes, it is the variance in the quality of mate that leads to shaping of sex roles, as evident that organisms exercise ‘choice’ in terms of discrimination based on morphology (Wang, 2002), age (Hansen and Price, 1995), competitive ability (Thornhill, 1993; Alcock, 2001) and mating status of the mate (Sakaluk *et al.*, 2002). Other perceivable phenotypic indicators like body size may also direct mate choice.

Body size indicates the physiological state and indirectly reflects good genes (Ryder and Siva-Jothy, 2001; Pech-May *et al.*, 2012). The role of size in male-male competition and female fecundity is well established (Bonduriansky, 2001). Studies considering ‘size’ as a criterion for mate discrimination and sexual selection are also recognised (Karsten *et al.*, 2009; Ellis and

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Bercovitch, 2011; Bowcock *et al*., 2013).

The advantages of body size has been conferred in insects as it is related to (1) fecundity (Blanckenhorn, 2000; Hodek *et al*., 2012; Omkar and Afaq, 2013), or (2) fast development and increased fitness of offspring (Katvala and Kaitala, 2001; Roff, 2002). Similarly for males, large size confer advantages in terms of (1) better fighting and competitive ability (Wedell and Karlsson, 2003; Filin and Ovadia, 2007) leading to increased chances of selection (Byrne and Rice, 2006; Joyce *et al*., 2009; Anjos-Duarte *et al*., 2011), and/or (2) larger ejaculates with more numbers of sperm (Bissoondath and Wiklund, 1996), nutrients and accessory gland proteins (Arnqvist *et al*., 2005; Avila *et al*., 2011), which influence sperm uptake (Eberhard, 1996; Wedell, 2005), remating propensity (Avila *et al*., 2011), fecundity, and offspring fitness (Vahed, 1998). However, larger size carries costs too, as larger individuals have longer developmental duration and are thus susceptible to increased risk of parasitism and predation (Blanckenhorn, 2000) owing to longer exposure (Abrams *et al*., 1996). Also, the individuals with large body size are not able to efficiently utilise energy under food stress (Gotthard *et al*., 1994; Blanckenhorn, 1998) and have decreased reproductive success in scramble competition as they are less agile. The strength of correlation between body size and reproductive success is also known to be modified by factors, *viz*. food (Dixon, 2007), presence of predators (Blanckenhorn, 1998), climate (Gotthard *et al*., 2007) and age (Xu and Wang, 2009; Amin *et al*., 2012).

Among ladybirds, the presence of size dependent preferential mating with respect to variation in dietary regime has been reported (Ueno *et al*., 1998; Perry *et al*., 2009), but there is no study evaluating the effect of adult size on shaping sex roles and its consequences on offspring fitness.

Keeping this in mind we carried out this study to investigate the effect of body size on (1) sex roles, (2) aspects of mating behaviour, (3) reproductive performance, (4) offspring development and adult longevity, and (5) sexual competitiveness of or preference for offspring of selected pairs as mates. All these aspects were investigated with the locally abundant, zigzag ladybird beetle, *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae).

2 MATERIALS AND METHODS

2.1 Insect

M. sexmaculatus is a polymorphic ladybird, with typical, intermediate and melanic morphs. The total developmental period (duration from egg to adult emergence) of the typical morph of *M. sexmaculatus* is 13.28 ± 1.00 days at 25 ± 2℃. The newly emerged adults when paired for a lifetime have a fecundity of 1 096.90 ± 75.64 eggs with egg viability of 62.10% ± 0.03% (Omkar and Bind, 2004).

2.2 Establishment of stock culture

Adults of typical morph of *M. sexmaculatus* (~30 of each sex; weighing 5 – 14 mg) were collected from the agricultural fields surrounding Lucknow, India (26°50′N, 80°54′E) and brought to the laboratory. The field collected adults were sexed and paired in plastic Petri dishes (9.0 cm × 2.0 cm), which were placed at 27 ± 1℃; 65% ± 5% RH; 14L: 10D photoperiod in environmental test chambers (CH-6S, Remi Instruments, Mumbai, India). They were provided with *ad libitum* supply of aphid, *Aphis craccivora* Koch (reared in glasshouse on *Vigna unguiculata* L. (Fabaceae) at 25 ± 2℃; 65% ± 5% RH). The pairs were checked daily for oviposition and eggs laid were isolated and inspected daily for hatching. Larvae hatched were placed in beakers (14.5 cm × 10.5 cm) in groups of ten per beaker and provided with *ad libitum* aphids till pupation and after adult emergence. This was continued across generations in order to raise a small laboratory population of adults. Fresh stocks were frequently added from the field to prevent inbreeding depression in the stock population.

2.3 Experimental protocol

2.3.1 Sub stock maintenance: Adults of mixed sizes were randomly selected from the stock, paired in transparent plastic Petri dishes (9.0 cm × 2.0 cm) containing daily replenished *ad libitum* supply of *A. craccivora*. The pairs were checked daily for oviposition and eggs laid were isolated and inspected daily for hatching. The emerging first instar larvae were reared until adult emergence in plastic beakers (14.5 cm × 10.5 cm, 5 individuals per beaker) and provided with *ad libitum* aphids till pupation and after adult emergence. The newly emerged adults were weighed on an electronic balance (Sartorius CP225-D: Sartorius AG, Goettingen, Germany) and segregated on the basis of their body mass, sexed and isolated in Petri dishes for use in experiments. The natural body mass variation in our stock ranged from 4 – 10 mg for males and 5 – 15 mg for females as has also been previously reported (Chaudhary *et al*., 2015). Males below 5 mg were considered as small (4.6 ± 1.6 mg; n = 70) while those above 9 mg were considered as large (9.1 ± 1.7 mg; n = 70).

Similarly females that weighed below 7 mg were considered as small (7.0 ± 1.6 mg; n = 70) while those above 12 mg were considered as large (12.0 ± 1.6 mg; n = 70). The difference in body mass of male and female of both sizes was statistically significant ($T_{\text{Male}} = 28.47$, $P = 0.000$ and $T_{\text{Female}} = 34.29$, $P = 0.000$).

2.3.2 Adult size and mate choice: To investigate the effect of adult body size on their chances of being selected as mates, four mate selection treatments were formed, *viz*. by (1) small males, (2) large males, (3) small females, and (4) large females.

In the first treatment, a 10-day-old small unmated male was introduced in a Petri dish (9.0 cm × 2.0 cm) and after five minutes two 10-day old virgin females (one small and one large) were simultaneously introduced into this Petri dish following Anjos-Duarte *et al*. (2011). For the next 30 minutes, the mating behaviour, which includes swift running, elytral fanning, contacts involving frequent touching and moving apart and first mounting attempt and culmination in genital contact with the accepted mate was observed and recorded. Females were also observed showing pronounced rejection or refrainment behaviour, which involved retracting the legs and making the body round, thereby dislodging the males. In cases where mating took place within 30 minutes, the unselected females were removed from the Petri dish and the mating was allowed to reach culmination. However, in instances, where no mating was established in the first 30 minutes, the trial was discarded and a fresh arena set up with new adults. As the males and females are not easily distinguishable in this ladybird beetle, the introduced adults were colour marked with small dots of non-toxic green and blue colour on the posterior edge of their right elytra, while, the adult to whom we gave the choice was kept unmarked. To prevent any bias in mate preference due to these colours, the marking was switched in each replicate.

Similar trial was also conducted for large males by providing simultaneous choice of small and large females. In treatment 3 and 4, 10-day-old virgin females were also provided with simultaneous choice of 10-day-old unmated small and large males. Each ladybird was used only once. Each mate choice treatment was replicated 20 times for a total of 80 mating observations involving 120 males and 120 females.

2.3.3 Effect of adult size on reproductive behaviour and output: In order to assess and compare the effect of body size on reproductive parameters in both preferred and non-preferred group, the following eight pairs obtained from the previous experiment were observed, (1) small male × large female; (2) small male × small female; (3) large male × large female; (4) large male × small female; (5) small female × large male; (6) small female × small male; (7) large female × large male; (8) large female × small male. Each of these combinations were studied in 17 replicates. In cases, where the pairs in a combination were not enough, additional pairs were added (for this two competitors of same size were placed in the mating trial and the mating pair resulting from this scenario was taken as a replicate). Each beetle was used only once. Mating parameters, such as time taken to commence mating (TCM) from the instant of cohabitation, latent period [(LP) (time between intromission and first abdominal shaking)] and copulation duration (time from intromission until dismounting) were recorded. After the termination of mating, the male was removed and the female was kept in a Petri dish on *ad libitum A. craccivora*. Daily oviposition and percent egg viability was recorded for five consecutive days for all treatments.

2.3.4 Adult size and offspring development and longevity: A total of 100 eggs from the first two days of oviposition from the all replicates per treatment mentioned above were selected randomly and placed in fresh plastic Petri dishes (5 eggs per Petri dish; 9.0 cm × 2.0 cm) under controlled abiotic conditions (27 ± 1℃, 65% ± 5% RH, 14L∶10D) until hatching. The first two days of oviposition was selected as it was our assumption that the maximum effect of mate preference would be visible in the initial oviposition. The incubation period and the number of larvae hatched were recorded. They were reared until adult emergence in plastic beakers (14.5 cm × 10.5 cm, 5 individuals per beaker) under standard laboratory conditions (27 ± 1℃, 65% ± 5% RH, 14L∶10D) and provided with *ad libitum A. craccivora* till pupation and after adult emergence. The total developmental duration was recorded. The percentage immature survival (number of adults emerged/number of the first instar larvae × 100) was also calculated for all treatments. On emergence the sexes were separated, weighed and kept singly in Petri dishes with daily replenished *ad libitum A. craccivora*. Along with this, the longevity of ten sets of unmated adults (each set had five males and five females) per treatment was also recorded.

2.3.5 Sexual competitiveness of offspring: Analysis of observations from experiment (a) (presented in results) revealed the higher success of large sized individuals as mates. In view of the contention of our hypothesis, that mate choice confers certain advantages to the offspring, we decided to test the sexual desirability/ competitive skills of offspring of selected pairs versus offspring of the laboratory stock, raised from the mating pairs given no mate choice. Size and age were kept similar to reduce any advantage due to them.

Thus, offspring from preferentially selected pairs (large × large and large × small) were sexed and isolated. They were reared separately for ten days. After this, these offspring were placed in mate choice trials with the offspring of laboratory reared pairs given no choice having same age and size. A 10-day-old small unmated male (laboratory reared) was given the simultaneous choice of small 10-day-old virgin (laboratory reared) and small female (mate choice reared). Similar trials were repeated with large laboratory reared males, who were given a choice between two large females (one laboratory reared and one mate choice reared). The female mate choice trial was carried out in a similar manner as described above. Choice was always given between same sized individuals so that size would not have any confounding effect. Each beetle was used only once. Each mate choice treatment was replicated 20 times for a total of 80 observations involving 120 males and 120 females.

2.4 Statistical analysis

The chi-square (χ^2) goodness-of-fit analysis was used to test the null hypothesis of random mating and for comparing the percentage of immature survival between all treatments. Data on mating and reproductive attributes, like time of commencement of mating, latent period, copulation duration, fecundity, egg viability, developmental duration and longevity acting as dependent factors were first tested for normal (Kolmogorov-Smirnoff) and homogeneous (Bartlett's) distribution. On being found normally distributed with homogeneous variation, above data (dependent factors) were subjected to two-way analysis of variance (ANOVA) with male and female body sizes as independent factors. The analysis was followed by comparison of means using *post hoc* Tukey's honest significance test at 5%. All statistical analyses were conducted using MINITAB-15 statistical software.

3 RESULTS

3.1 Adult size and mate choice

Larger adults attained higher mating success in both male and female mating trials of all sizes (Table 1). Statistically insignificant result was observed for first mounting attempts made by small males for the females of both sizes in small male mating trials. However, large males attempted mounting large females significantly more than small females in large male mating trials. In female mating trials also more number of large males attempted first mounting than small males, however, the result was statistically insignificant. Larger males achieved final copulation in significantly more number than small males in female mate choice trials (both sizes).

Table 1 Adult size and mating success in *Menochilus sexmaculatus*

Mate choice trial	Mating behaviour	
	First mounting attempt (by males)	Final copulation
Small male mate choice (N = 20)		
Large female	11	17
Small female	9	3
χ^2-value (P-value; df)	$\chi^2 = 0.40$ ($P = 0.527$; $df = 1$)	$\chi^2 = 19.600$ ($P = 0.001$; $df = 1$)
Large male mate choice (N = 20)		
Large female	14	18
Small female	6	2
χ^2-value (P-value; df)	$\chi^2 = 6.400$ ($P = 0.011$; $df = 1$)	$\chi^2 = 25.600$ ($P = 0.001$; $df = 1$)
Small female mate choice (N = 20)		
Large male	11	14
Small male	9	6
χ^2-value (P-value; df)	$\chi^2 = 0.40$ ($P = 0.527$; $df = 1$)	$\chi^2 = 6.400$ ($P = 0.011$; $df = 1$)
Large female mate choice (N = 20)		
Large male	12	15
Small male	8	5
χ^2-value (P-value; df)	$\chi^2 = 1.6$ ($P = 0.206$; $df = 1$)	$\chi^2 = 10.000$ ($P = 0.002$; $df = 1$)

3.2 Effect of adult size on reproductive behaviour and output

The results revealed noteworthy influence of body size on mating parameters in both male and female mate choice treatments. Lower value of TCM was observed when adults of similar sizes mated with each other in all the treatments (Fig. 1). Two-way ANOVA, however, revealed insignificant effect of size of male ($F = 1.53$, $P > 0.05$, $df = 1,67$), female ($F = 0.00$, $P > 0.05$, $df = 1,67$) and their interaction ($F = 0.65$, $P > 0.05$, $df = 1,67$) on TCM in male mating trials. In female mating trials size of male had insignificant influence on TCM ($F = 0.13$, $P > 0.05$, $df = 1,67$), while, female size ($F = 28.50$, $P < 0.0001$, $df = 1,67$) and their interaction ($F = 18.25$, $P < 0.0001$, $df = 1,67$) had significant effect on TCM.

Latent period decreased when larger adults were selected as mates by adults of both sizes and sexes (Fig. 1). Two-way ANOVA revealed insignificant effect of male and female size and their interaction on latent period in both male ($F_{Male} = 4.75$, $P > 0.05$, $df = 1,67$; $F_{Female} = 1.03$, $P > 0.05$, $df = 1,67$; $F_{Interaction} = 0.02$, $P > 0.05$, $df = 1,67$) and female mating trials ($F_{Female} = 0.44$, $P > 0.05$, $df = 1,67$; $F_{Male} = 0.86$, $P > 0.05$, $df = 1,67$; $F_{Interaction} = 0.02$, $P > 0.05$, $df = 1,67$).

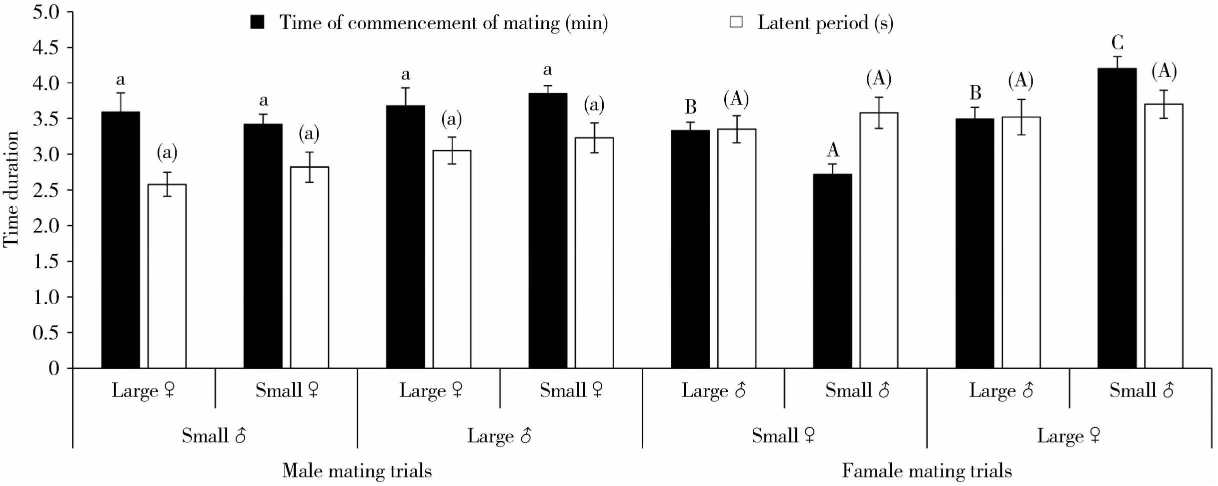

Fig. 1 Effect of adult size on time of commencement of mating and latent period in *Menochilus sexmaculatus*

Values are mean ± *SE*. Small open and closed letters denote comparison of means for male mating trials while large open and closed letters for female mating trials, respectively

Also, body size significantly influenced the copulation duration in both male ($F_{Male} = 10.79$, $P < 0.01$, $df = 1,67$; $F_{Female} = 58.16$, $P < 0.0001$, $df = 1,67$; $F_{Interaction} = 33.31$, $P < 0.0001$, $df = 1,67$) and female ($F_{Female} = 93.80$, $P < 0.0001$, $df = 1,67$; $F_{Male} = 18.13$, $P < 0.0001$, $df = 1,67$; $F_{Interaction} = 75.14$, $P < 0.0001$, $df = 1,67$) mate choice trial treatments. The longest copulation duration was recorded when large males mated with large females while shortest mating duration was observed when large males mated with small females (Fig. 2).

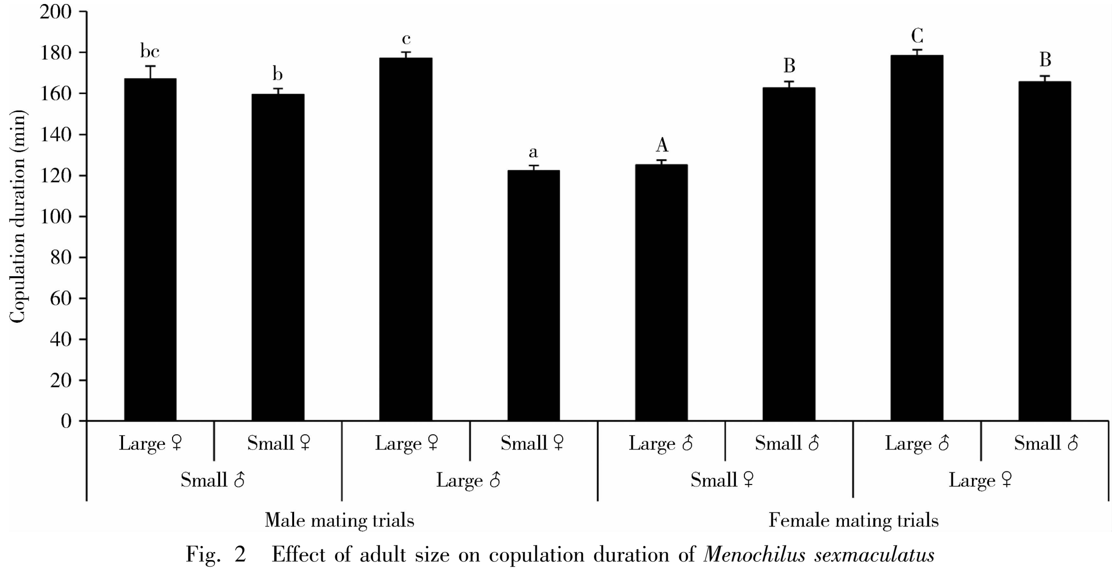

Fig. 2 Effect of adult size on copulation duration of *Menochilus sexmaculatus*

Values are mean ± *SE*. Small letters denote comparison of means for male mating trials while large letters for female mating trials, respectively.

Fecundity was affected by the size of females with large females laying significantly more eggs and this was irrespective of male size (Fig. 3). Two-way ANOVA revealed significant influence of female size on fecundity in both male ($F = 319.84$, $P < 0.0001$, $df = 1, 67$) and female ($F = 285.17$, $P < 0.0001$, $df = 1, 67$) mating trials, while, male size and interaction was found to be insignificant in both male ($F_{\text{Male}} = 0.53$, $P > 0.05$, $df = 1, 67$; $F_{\text{Interaction}} = 0.16$, $P > 0.05$, $df = 1, 67$) and female ($F_{\text{Male}} = 0.71$, $P > 0.05$, $df = 1, 67$; $F_{\text{Interaction}} = 1.56$, $P > 0.05$, $df = 1, 67$) mating trials. However, body size did not significantly influence egg viability in both male ($F_{\text{Male}} = 0.13$, $P > 0.05$, $df = 1, 67$; $F_{\text{Female}} = 2.76$, $P > 0.05$, $df = 1, 67$; $F_{\text{Interaction}} = 0.28$, $P > 0.05$, $df = 1, 67$) and female ($F_{\text{Female}} = 3.73$, $P > 0.05$, $df = 1, 67$; $F_{\text{Male}} = 0.22$, $P > 0.05$, $df = 1, 67$; $F_{\text{Interaction}} = 0.14$, $P > 0.05$, $df = 1, 67$) mate choice trials (Fig. 3).

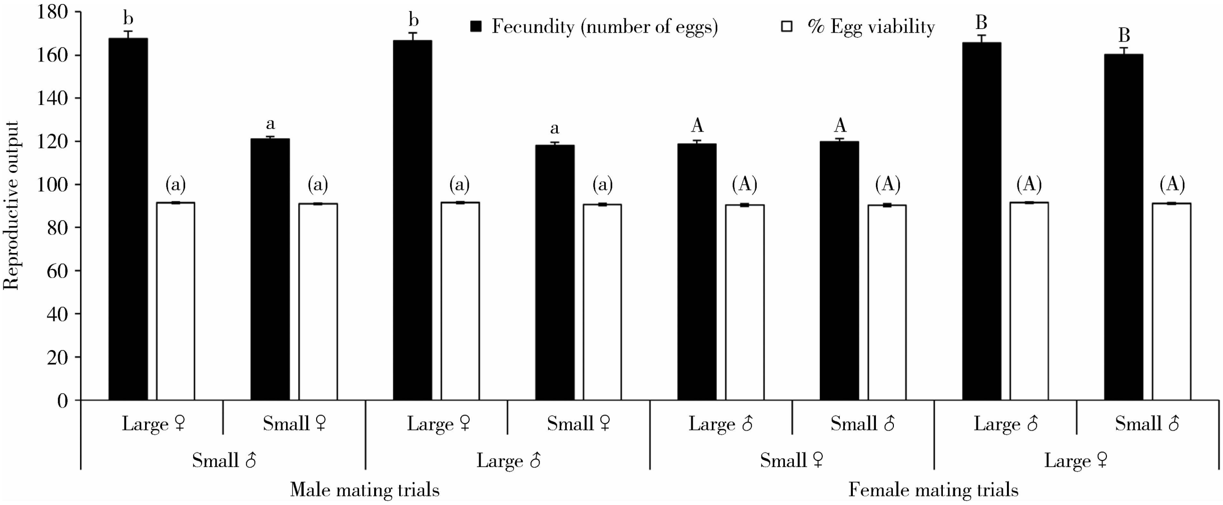

Fig. 3 Effect of adult size on erproductive output of *Menochilus sexmaculatus*

Values are mean ± *SE*. Small open and closed letters denote comparison of means for male mating trials while large open and closed letters for female mating trials, respectively.

3.3 Adult size and offspring development and longevity

The offspring of large adults developed significantly faster in both male and female choice trials than the offspring of small adults (Fig. 4). Two-way ANOVA revealed significant influence of adult size on total developmental duration in both male ($F_{\text{Male}} = 145.41$, $P < 0.0001$, $df = 1, 67$; $F_{\text{Female}} = 148.27$, $P < 0.0001$, $df = 1, 67$; $F_{\text{Interaction}} = 6.84$, $P < 0.05$, $df = 1, 67$) and female ($F_{\text{Female}} = 114.93$, $P < 0.0001$, $df = 1, 67$; $F_{\text{Male}} = 152.58$, $P < 0.0001$, $df = 1, 67$; $F_{\text{Interaction}} = 10.14$, $P < 0.01$, $df = 1, 67$) mate choice trials. The fastest development of offspring occurred when both the parents were large sized followed by the pairs having at least one large parent; with no significant difference in pairs with large males or large females as parents (Fig. 4). The comparison of percentage

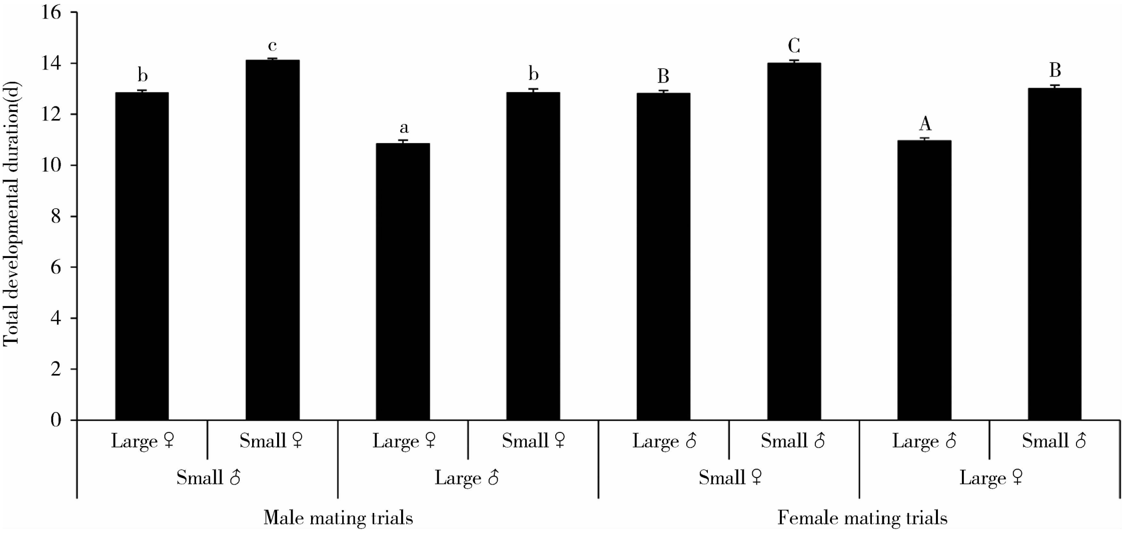

Fig. 4 Effect of parental size on total developmental duration of offspring of *Menochilus sexmaculatus*

Values are mean ± *SE*. Small letters denote comparison of means for male mating trials while large letters for female mating trials, respectively.

of immature survival between different treatments revealed no significant effect of parent body size ($\chi^2 = 6.28$, $df = 7$, $P = 0.50$).

The longevity of offspring was significantly influenced by the size of parents. In male mating trials, the male offspring of larger parents had significantly higher longevity (71.8 ± 0.73 days) than the male offspring of small parents (66.4 ± 0.67 days), while no difference was observed in longevities of male offspring sired by pairs in which either parent was large. Similar trend was found for the longevity of female offspring resulting from male mate choice trials (Table 2). In female mate choice trials the male (70.6 ± 0.67 days) and female (80.8 ± 0.58 days) offspring sired by larger pairs had higher longevity, while, the offspring sired by small-small or small-large pair had no significant difference in their longevities (Table 2).

Table 2 Effect of parental size on the longevity of offspring of *Menochilus sexmaculatus*

Mating pair		Longevity (d)	
Male size	Female size	Male mate choice	
		♂ Offspring	♀ Offspring
Small ♂	Large ♀	67.6 ± 0.81 a	76.6 ± 0.74 b
	Small ♀	66.4 ± 0.67 a	73.4 ± 0.74 a
Large ♂	Large ♀	71.8 ± 0.73 b	82.2 ± 0.58 c
	Small ♀	67.4 ± 0.74 a	74.4 ± 0.74 ab
F_{Male}		12.18**	21.56***
F_{Female}		14.13**	59.90***
$F_{\text{Interaction}}$		4.61*	10.48**
Female size	Male size	Female mate choice	
		♂ Offspring	♀ Offspring
Small ♀	Large ♂	67.8 ± 0.48 a	73.8 ± 0.58 a
	Small ♂	65.6 ± 0.74 a	72.2 ± 0.66 a
Large ♀	Large ♂	70.6 ± 0.67 b	80.8 ± 0.58 b
	Small ♂	67.4 ± 0.74a	73.4 ± 0.51 a
F_{Female}		11.63**	48.72***
F_{Male}		16.02**	58.70***
$F_{\text{Interaction}}$		0.55 NS	23.38***

Values are mean ± *SE*. Values followed by different letters show significant differences. *F*-values to be significant at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.0001$; $df = 1, 19$. Tukey's test range = 4.05. NS denotes *F*-values as not significant at $P > 0.05$.

3.4 Sexual competitiveness of offspring

The results revealed no significant preference for offspring sired by large individuals in the immediate next generation and neither were they sexually more competitive. In case of large offspring, no significant preference was found for adults of either origin (Table 3). Also, the small offspring of mate choice experiment did not achieve significant mating success against laboratory stock.

4 DISCUSSION

Theory of sexual selection predicts that variation in mate quality alter sex roles and thus mate choice (Edward and Chapman, 2011). In accordance with this, our study revealed the presence of male and female mate choice in relation to adult body size as a variance of mate quality. Males exhibited positive response to the indicator of female quality, *i. e.*, body size, and mated in significantly larger numbers. Females also mated with significantly more number of large males than small males and had higher reproductive success with them. The higher success achieved by large sized adults can be attributed to (1) a competitive advantage over smaller adults (passive mate choice) or (2) discrimination by females between mates on the basis of their quality as indicated by size (active mate choice). Two hypotheses propose how a female judges/chooses her mating partner: (1) Test hypothesis states that female assesses the quality of male actively by first showing rejection and if the male overcomes the attempted rejection, then he is considered fit and is accepted as mate, and (2) the rape hypothesis suggests that even if the female does not want to mate but the male is strong enough to subdue the rejection of female, mating occurs, as it is not in the interest of female to waste her energy in trying to reject such a male (Majerus, 1994).

The frequent contact and mounting attempts made by small males are indicative of their strategy opted under scramble competition where small males increase their reproductive success by attempting quick matings

Table 3 Influence of mate choice on sexual competitiveness of offspring in *Menochilus sexmaculatus*

Number of small males (laboratory stock)	Small females (laboratory stock)	Small females (mate choice experiment)	χ^2-value (*P*-value; *df*)
20	14	6	$\chi^2 = 6.40$ ($P = 0.011$; $df = 1$)
Number of large males (laboratory stock)	Large females (laboratory stock)	Large females (mate choice experiment)	
20	12	8	$\chi^2 = 1.60$ ($P = 0.206$; $df = 1$)
Number of small females (laboratory stock)	Small males (laboratory stock)	Small males (mate choice experiment)	
20	15	5	$\chi^2 = 10.00$ ($P = 0.02$; $df = 1$)
Number of large females (laboratory stock)	Large males (laboratory stock)	Large males (mate choice experiment)	
20	11	9	$\chi^2 = 4.00$ ($P = 0.527$; $df = 1$)

(Gotthard *et al.*, 2007). But, in the present study, the rejection shown by females towards small males in this ladybird beetle corroborates with the perception of being choosy. However, our result could not differentiate between the type of assortative mating, *i. e.*, 'true' or 'apparent' as the choice was just between small and large only (Arnqvist *et al.*, 1996). Studies on mating success accomplished by larger males (*e. g.*, Goulson *et al.*, 1993; Bonduriasky, 2001; Beeler *et al.*, 2002; Omkar and Afaq, 2013) and females (Omkar and Afaq, 2013) have also been previously reported in other insects. Mate choice in favour of large sized mates can be attributed to the reproductive gains due to (1) direct material benefits such as increased nuptial gifts, fecundity or parental care (Andersson, 1994; Arnqvist and Nilsson, 2000) in the present generation or (2) indirect genetic benefits such as enhanced offspring fitness or attractive sons (Hine *et al.*, 2002; Rundle *et al.*, 2007; Cothran, 2008) for their offspring in subsequent generation (Andersson, 1994).

The higher fecundity in pairs having larger females regardless of the size of male she mated to is indicative of the fact that possibly fecundity is governed by the size of female and males just add quality to the eggs by affecting their viability. According to Darwin (1874), the evolution of large body size in females is favoured because the larger females produce more offspring and this has been reported in many studies (Bonduriansky, 2001; Roff, 2002; Berger *et al.*, 2008; Salavert *et al.*, 2011).

In contrast to previous studies which report a positive effect of male size on egg viability in insects (Yadav *et al.*, 2010; Omkar and Afaq, 2013) including the ladybirds (Bista and Omkar, 2013), we found no direct benefit of larger males on the egg viability, though an indirect benefit was found on the rate of development of offspring. This could be attributed to the reason that ageing has more pronounced effect on egg viability (Tan *et al.*, 2013) rather than body size/other traits and as in the experiment the age of adults of both sexes and sizes had been kept constant; no significant influence on egg viability was observed.

The effect of large body size of parents on developmental duration of offspring could be ascribed to better genes (Kokko *et al.*, 2006), larger ejaculates by males with more numbers of sperm (Bissoondath and Wiklund, 1996), more nutrients via accessory gland proteins (Avila *et al.*, 2011), more yolk and other nutrients in eggs (Omkar and Afaq, 2013). Studies show that progeny fitness may also change on the basis of differential investment in eggs by females in response to male quality (Cunningham and Russell, 2000; Prokop *et al.*, 2007) and nutrients provided by them. Our results on increased longevity of offspring sired by large parents are indicative of the possible increased fitness they might have gained through some indirect genetic benefit from their parents.

A few studies have shown that progeny of sexually selected parents achieved more mating success (Wedell and Tregenza, 1999; Rundle *et al.*, 2007). However, we did not observe any such benefits in terms of their preferential selection or higher sexual competitiveness as mates. This could be attributed to the fact that genetic benefits of mate choice probably appear after considerable time in the progeny unlike direct benefits such as fecundity, viability, *etc.*, which are obtained immediately after selection. However, if the number of replicates and the number of generations which undergo such selection are increased, then possibly significant effects of mate choice may be found in the preferential selection or increased sexual competitiveness of the offspring.

Thus, from this study it could be concluded that: (1) when given simultaneous choice of mates differing in quality both the sexes exercised mate choice, *i. e.*, presence of mutual mate choice, (2) body size served to be an honest indicator of reproductive fitness for both the sexes, (3) the higher success of larger adults could be due to either active mate choice or passive one or both might be operating, (4) refrainment to mating attempts of small males by females is suggestive of them being choosy, (5) large females produced more eggs than did small females regardless of paternal size, and body size, however, did not influence egg viability, (6) mate choice affects offspring development and longevity, and (7) the offspring of larger parents were not significantly preferred as mates over the offspring from the laboratory stock in the immediate next generation.

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成虫体型大小驱动六斑月瓢虫性间相互选择

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摘要:【目的】配偶选择是性选择的中心过程,当繁殖成本发生波动和配偶质量存在差异时,传统的性别作用也随之不同。为了验证在某些条件下雄性也可以像雌性一样进行选择,我们研究了雄性和雌性六斑月瓢虫 *Menochilus sexmaculatus* (Fabricius)的交配成功率与作为适合度指标的成虫体型大小之间的关系。【方法】从初始种群中随机选择体型小和体型大的两性成虫,进行雄性和雌性配偶选择试验。并对成功交配的各个配对组的后代也进行配偶选择试验,测试其交配成功率。【结果】配偶选择试验结果表明,在雄性和雌性交配试验中交配的成功取决于体型大小。雄性根据其品质即体型大小这一繁殖力指标对雌性进行区分。同样,在雌性交配试验中体型大的雄虫比体型小的雄虫交配成功率高。无论亲本体型如何,体型大的雌虫都比体型小的雌虫产卵量高;不过,体型大小不影响卵的存活力。体型大的亲本的后代比体型小的亲本的后代发育更快,寿命更长,但是将其与来自初始种群的后代进行配偶选择时,它们在性合意(sexual desirability)或竞争力方面没有表现任何优势。【结论】六斑月瓢虫中存在以体型大小为目的性状的相互配偶选择。

关键词: 六斑月瓢虫; 适合度; 配偶选择; 交配成功; 繁殖产量; 性竞争

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